

True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon

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Abstract. In coastal systems, marine-protected areas (MPAs) have been shown to increase the diversity, abundance, and biomass of wildlife assemblages as well as their resilience to climate change. The effectiveness of pelagic MPAs is less clear, with arguments against their establishment typically based on the highly mobile nature of pelagic taxa. We used mid-water stereo-baited remote underwater video systems (stereo-BRUVS) and spatial predictive models to characterize the pelagic wildlife assemblage at the head of the Perth Canyon, one of the largest submarine canyons in Australia, over a 7-yr period (2013–2019). The total number of unique taxa and mean values of taxonomic richness, abundance, fork length, and biomass demonstrated strong inter-annual stability, although mean taxonomic richness and abundance were significantly lower in 2018 relative to other years. Seasonal variability was absent in 2016, but in 2018, taxonomic richness and abundance were three times greater in the Austral spring than in the autumn. Some mobile megafauna were only recorded at the Perth Canyon Marine Park (PCMP) in the autumn, suggesting a seasonal component to their occurrence. The fine-scale distribution of pelagic taxa at the canyon head was largely stable over time, with many areas of higher relative probability of presence located outside protected zones. Despite a degree of variability that may relate to the effect of the El Niño Southern Oscillation on the Leeuwin Current, the PCMP assemblage demonstrates a relatively high degree of spatiotemporal stability. Stronger protection of the PCMP (IUCN II or higher) would potentially improve conservation outcomes for many species of pelagic wildlife.

Key words: annual and seasonal variability; mid-water stereo-BRUVS; marine-protected areas; pelagic fish and sharks; Perth Canyon; Western Australia.

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INTRODUCTION

The pelagic zone is one of the least protected ecosystems on Earth, and its sharks and rays are among the most at risk vertebrates, with almost a quarter of species designated as endangered, vulnerable, or near threatened by the International Union for Conservation of Nature (IUCN) Red List (Dulvy 2014, Dulvy et al. 2017). Top pelagic predators such as the hammerhead shark

Sphyrna sp. have been reduced in abundance to 2–10% of pre-industrial fishing levels, and few spatial refuges remain (Myers et al. 2007, Letesier et al. 2019, Queiroz et al. 2019). The inherent noisiness of fisheries data, a lack of standardized and/or species level data and widespread lack of transparency in some parts of the fishing industry, means that the magnitude of these declines remains debated (Beddington et al. 2007). However, the cross-taxa nature of the downward

population trajectories of sharks, tuna, and other pelagic predators is clear (Juan-Jordá et al. 2011, Dulvy 2014, Palomares et al. 2020). Efforts to manage and/or reverse these declines have largely failed thus far (Pauly 2018), with only few exceptions (Neilson et al. 2013).

There is now strong evidence that coastal MPAs increase the density and biomass of sharks (Bond et al. 2012, Frisch and Rizzari 2019) and other marine taxa (Lester and Halpern 2008, Marshall et al. 2019), including mobile species (Kerwath et al. 2008). MPAs also create spillover effects that boost adjacent fisheries and biodiversity (Kerwath et al. 2013, Di Lorenzo et al. 2016), and increase ecological resilience to climate change (Bates et al. 2013, Davies et al. 2017, Roberts et al. 2017). There is some evidence that pelagic MPAs, similarly, can benefit mobile species (Jensen et al. 2010, Boerder et al. 2017, Doherty et al. 2017), although this is still debated (Le Quesne and Codling 2009, Sibert et al. 2012). Small, strategically placed MPAs can benefit mobile species, especially when local fishing pressures are high (Kerwath et al. 2008, Mee et al. 2017) and large pelagic MPAs such as the British Indian Ocean Territory MPA have been shown to encompass the activity spaces of blue marlin *Makaira nigricans*, sailfish *Istiophorus platypterus*, silky sharks *Carcharhinus falciformis*, and yellowfin tuna *Thunnus albacares* (Carlisle et al. 2019).

A traditional argument against the implementation of pelagic MPAs is that they are difficult and/or prohibitively expensive to enforce (Game et al. 2009, Kaplan et al. 2010). Moreover, many pelagic species are highly mobile and often follow spatially dynamic hydrographic features such as fronts, traveling up to thousands of kilometers in a year (Kaplan et al. 2010, Runge et al. 2014). Thus, pelagic MPAs may only protect a fraction of a species' life cycle, and it has been argued that dynamic pelagic MPAs would have greater conservation benefits than traditional, static MPAs (Hobday et al. 2014, Garcia-Rojas et al. 2018, Gilman et al. 2019). However, pelagic megafauna also display broad predictability in their movement patterns. Sharks and other pelagic wildlife such as the black marlin *Istiompax indica* may display natal or regional philopatry, revisiting the same locations over time (Jorgensen et al. 2010, Howey-Jordan et al. 2013, Rogers et al. 2015). Mobile species also tend to

migrate along prescribed highways (Horton et al. 2017, Sequeira et al. 2018) and use submarine canyons and other locations of topographical complexity as reliable and predictable foraging grounds (Bouchet et al. 2017, Boerder et al. 2019, Gilman et al. 2019).

Despite being one of the least explored ecosystems on the planet (Matos et al. 2018), submarine canyons are keystone structures that strongly influence the distribution of pelagic wildlife (Vetter et al. 2010, Santora et al. 2018). Submarine canyons provide refugia from predators in otherwise homogeneous and exposed shelf and slope environments (Fernandez-Arcaya et al. 2017, Jones et al. 2019). Their complex bathymetry interacts with currents to generate upwellings, fronts, internal waves, and sub-surface eddies that inject nutrients into the euphotic zone, creating primary production hotspots that concentrate krill and other small prey for larger, mobile predators (Bax and Hedge 2015, Huang et al. 2018, Santora et al. 2018). Shelf-incising submarine canyons are of particular ecological importance because they allow the direct transfer of cold, nutrient-rich water into the neritic zone (Santora et al. 2018).

One example of such a submarine canyon is the Perth Canyon in Western Australia. Carved over 100 million years ago by an ancient river in Western Australia, the 4683 m deep Perth Canyon is the second largest submarine canyon on Australia's continental margin (Huang et al. 2014). Over 75% of the canyon's depth range lies in darkness and its vertical cliffs, 600 m tall in places, support a diverse range of invertebrates and coral graveyards dating to the last ice age (Trotter et al. 2019). The head of the Perth Canyon lies approximately 60 km west of Perth, which is the capital and largest regional population center of Western Australia. At the canyon head, which lies in 281 m of water, ROV surveys have revealed a benthos dominated by crabs, polychaete tube worms, glass sponges, and lobsters while grenadiers and deep-sea dories are the most common demersal fish species (Trotter et al. 2019).

The water column of the Perth Canyon consists of several major water masses, including the Leeuwin Current, a warm (16–24°C) surface layer, the Leeuwin Undercurrent, a deeper, northward-flowing and nutrient-rich layer, and Upper Circumpolar Deep Water, a 2 km deep

water mass that originates in Antarctica (Rennie et al. 2009, Trotter et al. 2019). Inter-current shear and a strong interaction between the canyon and the Leeuwin Undercurrent generate deep cyclonic eddies and internal waves, causing upwelling, the formation of a high-productivity, sub-surface layer (Rennie et al. 2009, Huang et al. 2014), and aggregations of pygmy blue whales *Balaenoptera musculus brevicauda* and other mobile megafauna (Rennie et al. 2009, Erbe et al. 2015, Bouchet et al. 2017, Trotter et al. 2019). Moreover, this upwelling occurs throughout the year to some extent, such that the Perth Canyon may act as a year-round foraging ground for some species (Pattiaratchi and Buchan 1991, Feng et al. 2009, Rennie et al. 2009, Nanson et al. 2018).

In 2012, almost 2.4 million km², or 36% of Australia's ocean, was given marine park status, including the 7409 km² Perth Canyon Marine Park (PCMP). However, in 2013, the newly elected government suspended the marine parks plan and commissioned an independent review that was eventually published in 2016. When the management plans were finally implemented in July 2018, the level of protection afforded to the head of the Perth Canyon had been downgraded from the originally planned IUCN II (i.e. no fishing) zoning to IUCN IV zoning which allows both recreational and commercial fishing and limits protection to the sea floor habitat.

Mid-water stereo-baited remote underwater video systems (stereo-BRUVS) are increasingly used to document pelagic assemblages as an alternative to lethal, fisheries-based sampling, particularly in MPAs (Letessier et al. 2019, Bouchet et al. 2020). Here, we use a long-term stereo-BRUVS dataset collected between 2013 and 2019 to assess the potential conservation value of the area in terms of the predictability of its aggregations of wildlife. Specifically, we test the hypothesis that the assemblage at PCMP does not display significant variation in total unique taxa, taxonomic richness, abundance, biomass, and size between years, that is, displays sufficient spatiotemporal stability to warrant stronger protection (Fig. 1). We also model the probability of occurrence of pelagic taxa at the canyon head, predicting that fine-scale spatial trends are largely consistent over time.

The study builds on an initial analysis at this location that predicted the probability of

occurrence of pelagic taxa in and around the canyon head (Bouchet and Meeuwig 2015), with the aim of establishing whether current levels of protection are commensurate to the conservation importance of this site to pelagic taxa. Our hypothesis that the PCMP would display temporal stability in these characteristics was underpinned by evidence that (1) upwelling, and therefore, potentially favorable prey conditions likely occur year-round at the canyon (Pattiaratchi and Buchan 1991, Rennie et al. 2009, Nanson et al. 2018), and (2) Perth Canyon is used as a foraging ground and/or navigational marker by several iconic marine megafauna, including cetaceans and shark species such as the tiger shark *Galeocerdo cuvier* and the shortfin mako *Isurus oxyrinchus* (Ferreira et al. 2015, Corrigan et al. 2018).

METHODS

Mid-water stereo-BRUVS

Mid-water stereo-BRUVS were deployed in strings of five rigs, with each rig on a string separated by 200 m of line (Appendix S1: Fig. S1; Bouchet et al. 2018). The data from 2013 were sourced from Bouchet and Meeuwig (2015), although in that study the rigs were not joined in longline configurations but still drifted largely in parallel. String is defined as the sampling unit, noting that individual rigs are not statistically independent because they are deployed from a single point of entry. The longline configuration, or string, simplifies retrieval and minimizes loss of equipment. Rigs were deployed for a minimum of two hours and then retrieved. The surveys were conducted from the vessels *RV Whale Song*, *Thalanyji*, and *NEGU* under an exemption from the Australian Marine Safety Authority (EX2016/A185; EX2017/A007A). All fieldwork was approved under ethics permit RA/3/100/1484.

Field sampling design

Sampling sites were chosen based on a generalized random tessellation stratified design (Fig. 1), with a focus on the area of the PCMP that lies in and adjacent to the canyon head. Austral autumn was considered to span the period between April and June, with Austral spring occurring between October and December

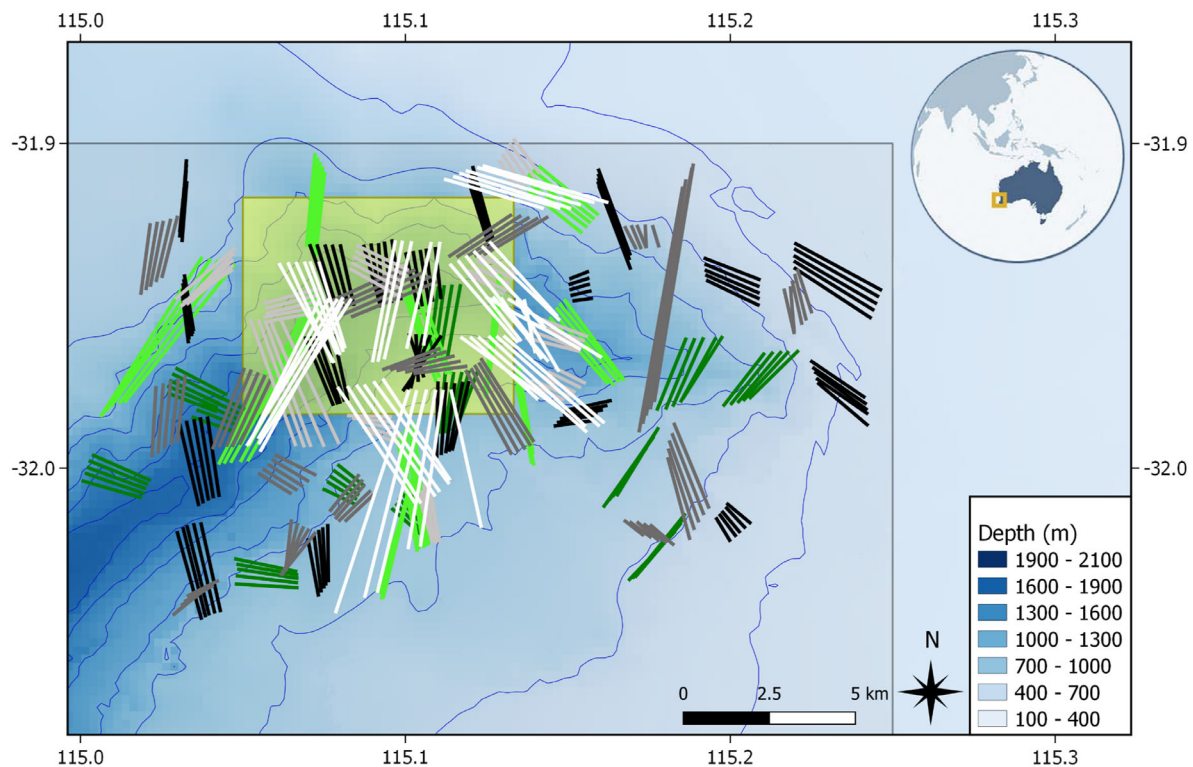


Fig. 1. Deployments of mid-water stereo-BRUVS at the head of Perth Canyon in autumn 2013 (white), autumn 2016 (light gray), spring 2016 (light green), autumn 2018 (dark gray), spring 2018 (dark green), and autumn 2019 (black) with the internal yellow shaded box representing the boundary of the current IUCN IV zone and the larger, gray box representing the outer perimeter of the PCMP (IUCN VI).

(Sequeira et al. 2012). Replicating the autumn 2013 survey conducted by Bouchet and Meeuwig (2015), surveys were conducted in the autumn of 2016, 2018, and 2019 while spring surveys occurred in 2016 and 2018. The spring 2018 and autumn 2019 surveys were the only ones to be conducted after enforcement of the MPA began in July 2018. A total of 398 rigs were deployed as part of 78 strings, with an average of 13 strings deployed per survey across seabed depths ranging from 172 to 1550 m (Appendix S1: Table S1). Because the 2013 rigs largely drifted together from the point of deployment, group deployments were treated as strings. All sampling was undertaken during daylight hours between 7:00 and 17:00 to minimize any effects of crepuscular and nocturnal behavior on fishes (Axenrot et al. 2004), which may bias our interpretation of results.

Image analysis

Videos were imported into the Event Measure software package (SeaGIS Pty) for processing. Processing commenced once the rig stabilized at a depth of 10 m below the sea surface and ended after two hours. Animals were identified to species level where possible and to genus or family otherwise. We estimated relative abundance as the maximum number of individuals of a given taxa in a single frame (Cappo et al. 2006; MaxN). We also took fork length measurements that generated estimates of distance of individual animals from the rig. Lengths were converted to weight using taxa-specific length–weight relationships derived from FishBase (Froese and Pauly 2020) and then summed to estimate biomass. Image analysis included independent checks on taxa identifications performed by experienced analysts.

Data analysis

Taxonomic richness, abundance, biomass, and fork length.—A taxa accumulation curve was calculated for combined surveys using string as the sampling unit and the Michaelis-Menten model to estimate the pool size and the number of samples needed to record 50% of the taxa (Keating and Quinn 1998). The total unique number of taxa observed on a string (TR_U) was calculated as the sum of taxa found on any given rig across a string. Taxonomic richness (TR), total abundance (TA), total biomass (TB; kg; excluding three common minke whales *Balaenoptera acutorostrata*), and mean fork length (FL; cm) were calculated for each rig, with TA, TB, and FL then log-10-transformed to meet the assumption of homoscedasticity (Zar 2010). Finally, TR, logTA, logTB, and logFL were averaged to generate mean values for each string as the sampling unit.

Interannual and seasonal variation in TR_U , TR, TA, TB, and FL was tested using permutational analysis of variance (PERMANOVA) based on unrestricted permutations, with survey as the fixed factor (Zar 2010, Anderson 2017). All analyses were conducted using software Primer v.7 (Clarke and Gorley 2020). For each univariate variable, a Euclidean distance matrix was calculated. The multivariate taxa abundance data were square-root-transformed and a Bray-Curtis resemblance matrix then calculated. The Bray-Curtis resemblance matrix was chosen as it is not influenced by joint-zeros (Anderson 1997), which reduces the influence of samples with no observations. For both the univariate and multivariate data, one-way PERMANOVA was used to test for an effect of year on TR_U , TR, TA, TB, and FL. As the surveys were imbalanced (four autumnal vs. two spring surveys), only the autumn data from the four years were used to control for seasonal effects. Where one-way PERMANOVA results were significant, pairwise tests were used to determine which years were responsible for the differences.

Two-way PERMANOVA was used to test the effect of year and season on the same assemblage variables listed above, based on the balanced autumn and spring data for 2016 and 2018. Where the interaction was insignificant, it was removed and the PERMANOVA recalculated (Zar 2010). No pairwise tests were necessary as each factor only had two levels. For the

taxonomic assemblage data, a canonical analysis of principal co-ordinates (CAP) was also used to visualize the distinctiveness of the pelagic taxa in multivariate space (Anderson 2008).

Fine-scale spatial and temporal stability

To determine whether the spatial distribution of taxa was consistent in time, we built presence-only maximum entropy (MaxEnt) models of wildlife occurrence (Phillips et al. 2006, Bouchet and Meeuwig 2015) in statistical software package R v3.4.3 (R Core Team 2019). We considered an identical set of candidate explanatory variables (depth, aspect northing, rugosity, longitudinal curvature, cross-sectional curvature, slope, slope variance, topographic position index, fractal dimension, and sea surface temperature mean and variance), in addition to daytime remote-sensed chlorophyll *a* (mg/m^3), derived from 8-day AQUA MODIS composite images available at 4 km resolution (Bouchet and Meeuwig 2015). Rugosity was included as a variable due to its well-understood influence on surface productivity and prey availability, via upwelling, eddy formation, and diurnally migrating species (Rennie et al. 2009, Bouchet et al. 2017, Maggs et al. 2019). Temperature and chlorophyll *a* values were sourced from the Environmental Data Connector (<http://www.pfeg.noaa.gov/products/EDC/>) and both seasonal means and variances calculated.

Observations of pelagic taxa were pooled and thinned to reduce the effects of spatial auto-correlation and improve potential model performance (Verbruggen et al. 2013). We used the ENMEval package (Muscarella et al. 2014) for tuning, allowing optimal feature classes (linear vs. quadratic) and regularization multipliers (β , from 1 to 8 in one-unit increments) to be chosen automatically according to Akaike's second-order information criterion score (AIC_c ; Sequeira et al. 2012). We then identified the most relevant predictors using iterative functions from the MaxentVariableSelection package (Jueterbock et al. 2016), run at a contribution threshold of 5%. Reduced models were implemented using the R package dismo (Hijman et al. 2016), using 1000 background (pseudo-absence) points, randomly extracted based on a custom bias grid as defined by Bouchet and Meeuwig (2015) and rescaled to range between 1 and 20 (Elith et al. 2010). Models were trained on 75% random partitions of the

data (repeated $n = 50$ times), reserving the remaining 25% for performance evaluation based on the true skill statistic (Allouche et al. 2006). We interpreted MaxEnt's logistic output as a measure of relative occurrence probability and mapped final predictions across the region of study.

To ensure robust comparisons of spatial patterns across time periods, we truncated model predictions made in areas characterized by novel conditions relative to the training data, using the multivariate environmental similarity surface (MESS) tool (Elith et al. 2011). This tool quantifies the distance in environmental space between each prediction pixel and the set of reference points contained in the original sample (Dormann et al. 2007, Fitzpatrick and Hargrove 2009). To improve the credibility of the model predictions, we computed MESS indices for each survey, and only retained those intersecting grid cells that yielded positive MESS values in all years (Elith et al. 2011, Verbruggen et al. 2013). We then compared maps based on a structural similarity index (SSIM, ranging from -1 to $+1$), with SSIM values typically used qualitatively rather than in the context of explicit thresholds (Robertson et al. 2014, Jones et al. 2016). A value of -1 indicates complete dissimilarity between the spatial structure of the maps, 0 indicates that species distributions are independent and 1 shows that the maps are identical (Robertson et al. 2014, Jones et al. 2016).

RESULTS

Taxonomic richness, abundance, biomass, and fork length

The taxa accumulation curve for the combined survey data based on 78 strings indicated a taxonomic pool of 40, with 16 samples required to capture 50% of the pool. In total, 1,467 individuals representing 32 taxa and 19 families or classes were recorded. We also recorded 105 unidentified teleost juvenile fishes (defined as translucent and typically <2 cm in fork length), noting that accurate identification of most larval fish species based on morphology is largely impossible during early life stages (Ko et al. 2013). The most common observed taxa included the following: Decapterus scad *Decapterus* sp. (31% of total mean abundance), jacks Carangidae sp. (20%), common dolphinfish *Coryphaena hippurus* (9%),

and juveniles (9%). Observed fishes ranged in size from 0.5-cm-long juveniles to a 5.3-m-long northern minke whale (Tables 1, 2).

One-way PERMANOVA demonstrated that the autumnal assemblage in the study area did not vary between years in terms of TR_U, TB, or FL (Fig. 2; Table 3). However, both TR (pseudo- $F = 4.49$, $P = 0.009$) and logged TA differed

Table 1. Family, scientific name, and common name for pelagic taxa recorded in the PCMP across all surveys, ordered alphabetically by family.

Family	Scientific name	Common name
Balaenopteridae	<i>Balaenoptera acutorostrata</i>	Northern minke whale
Carangidae	Carangidae sp	Jacks
	<i>Decapterus</i> sp	Decapterus scad
	<i>Naucratus ductor</i>	Pilotfish
	<i>Seriola lalandi</i>	Yellowtail amberjack
Carcharhinidae	<i>Carcharhinus brachyurus</i>	Copper shark
	<i>Carcharhinus falciformis</i>	Silky shark
	<i>Carcharhinus</i> sp	Requiem shark
	<i>Galeocerdo cuvier</i>	Tiger shark
	<i>Prionace glauca</i>	Blue shark
Hydrozoa (class)	Hydrozoa sp	Sea jellies
Coryphaenidae	<i>Coryphaena equiselis</i>	Pompano dolphinfish
	<i>Coryphaena hippurus</i>	Common dolphinfish
Delphinidae	<i>Delphinus delphis</i>	Common dolphin
Echeneidae	<i>Echeneis naucrates</i>	Live sharksucker
	<i>Remora remora</i>	Shark sucker
Fistulariidae	<i>Fistularia</i> sp	Cornetfish
Istiophoridae	<i>Istiompax indica</i>	Black marlin
Lamnidae	<i>Isurus oxyrinchus</i>	Shortfin mako
Molidae	<i>Mola mola</i>	Ocean sunfish
Monacanthidae	<i>Aluterus monoceros</i>	Unicorn leatherjacket filefish
	Monacanthidae sp	Leatherjackets
Myliobatidae	<i>Mobula</i> sp	Mobula ray
Nomeidae	<i>Psenes</i> sp	Psenes driftfish
Scombridae	<i>Acanthocybium solandri</i>	Wahoo
	<i>Katsuwonus pelamis</i>	Skipjack tuna
	<i>Thunnus maccoyii</i>	Southern bluefin tuna
	<i>Thunnus</i> sp	Thunnus tuna
Sphyrnidae	<i>Sphyrna</i> sp	Barracudas
Sphyrnidae	<i>Sphyrna mokarran</i>	Great hammerhead
Syngnathidae	Syngnathidae sp	Pipefishes
Tetraodontidae	<i>Arothron firmamentum</i>	Starry toado
Juvenile	Juvenile sp	Juvenile

Table 2. Common names for pelagic taxa recorded in the PCMP across all surveys, with total number of sightings (n), mean number of sightings per string (n mean), and average fork lengths (FL; cm), ordered alphabetically by common name. Ellipses indicate where no observations of a taxa were recorded.

Common name	Autumn								Spring				FL (cm)
	2013		2016		2018		2019		2016		2018		
	<i>n</i>	<i>n</i> mean	<i>n</i>	<i>n</i> mean	<i>n</i>	<i>n</i> mean	<i>n</i>	<i>n</i> mean	<i>n</i>	<i>n</i> mean	<i>n</i>	<i>n</i> mean	
Barracuda	1	0.11
Black marlin	...	-	1	0.09	198.2
Blue shark	1	0.11	272.9
Common dolphin	7	0.41	204.9
Common dolphinfish	48	5.33	21	2.10	19	1.12	102	5.37	8	0.73	12	1.00	68.6
Copper shark	2	0.12	7	0.37	196.6
Cornetfish	2	0.20	1	0.06	1	0.05	18.8
Decapterus scad	199	22.11	81	8.10	19	1.12	151	7.95	38	3.45	118	9.83	5.78
Great hammerhead	1	0.06	270
Jacks	4	0.44	30	1.76	3.26
Juvenile	62	6.20	5	0.29	3	0.16	35	3.18	-	-	2.9
Leatherjackets	4	0.36	5	0.42	3.21
Live sharksucker	1	0.06
Mobula ray	1	0.09
Northern minke whale	3	0.30	470
Ocean sunfish	2	0.22
Pilotfish	36	4.00	4	0.40	2	0.12	4	0.21	2	0.18	1	0.08	13.2
Pipefishes	1	0.09
Pompano dolphinfish	2	0.12
Psenes driftfish	4	0.44	3	0.27	1	0.08	12.3
Requiem shark	1	0.08	...
Sea jellies	1	0.06
Shark sucker	6	0.67
Shortfin mako	1	0.11	3	0.27	140.9
Silky shark	1	0.11	204.9
Skipjack tuna	2	0.20	-	-	13	0.68	45
Southern bluefin tuna	15	0.88	18	0.95	36.8
Starry toado	3	0.16	38.5
Thunnus tuna	8	0.89
Tiger shark	2	0.11	191.4
Unicorn leatherjacket filefish	1	0.06	28.6
Wahoo	2	0.18	202
Yellowtail amberjack	22	1.83	44.1

between years (pseudo- $F = 5.39$, $P = 0.002$). Pairwise comparisons (Appendix S1: Table S2) confirmed that 2018 differed from all other years for both TR (2013 $t = 3.27$, $P = 0.005$; 2016 $t = 3.13$, $P = 0.005$; 2019 $t = 2.92$, $P = 0.006$) and logged TA (2013 $t = 3.76$, $P = 0.001$; 2016 $t = 3.2$, $P = 0.004$; 2019 $t = 3.78$, $P = 0.003$), and in both cases, TR and TA values in 2018 were on average roughly 50% of those in the other years. Mean TR, for example, was 0.6 taxa per survey ± 0.10

in 2018, compared to 1.29 ± 0.21 in 2013, 1.34 ± 0.24 in 2016, and 1.1 ± 0.13 in 2019 (Appendix S1: Table S3).

Autumn and spring surveys differed significantly in terms of TR_U (pseudo- $F = 4.29$, $P = 0.048$), TR (pseudo- $F = 11.4$, $P = 0.001$), TA (pseudo- $F = 17.2$, $P = 0.001$), and FL (pseudo- $F = 5.46$, $P = 0.034$). There was an interaction between year and season for all variables except TR_U (Table 3, Fig. 2). Spring was always

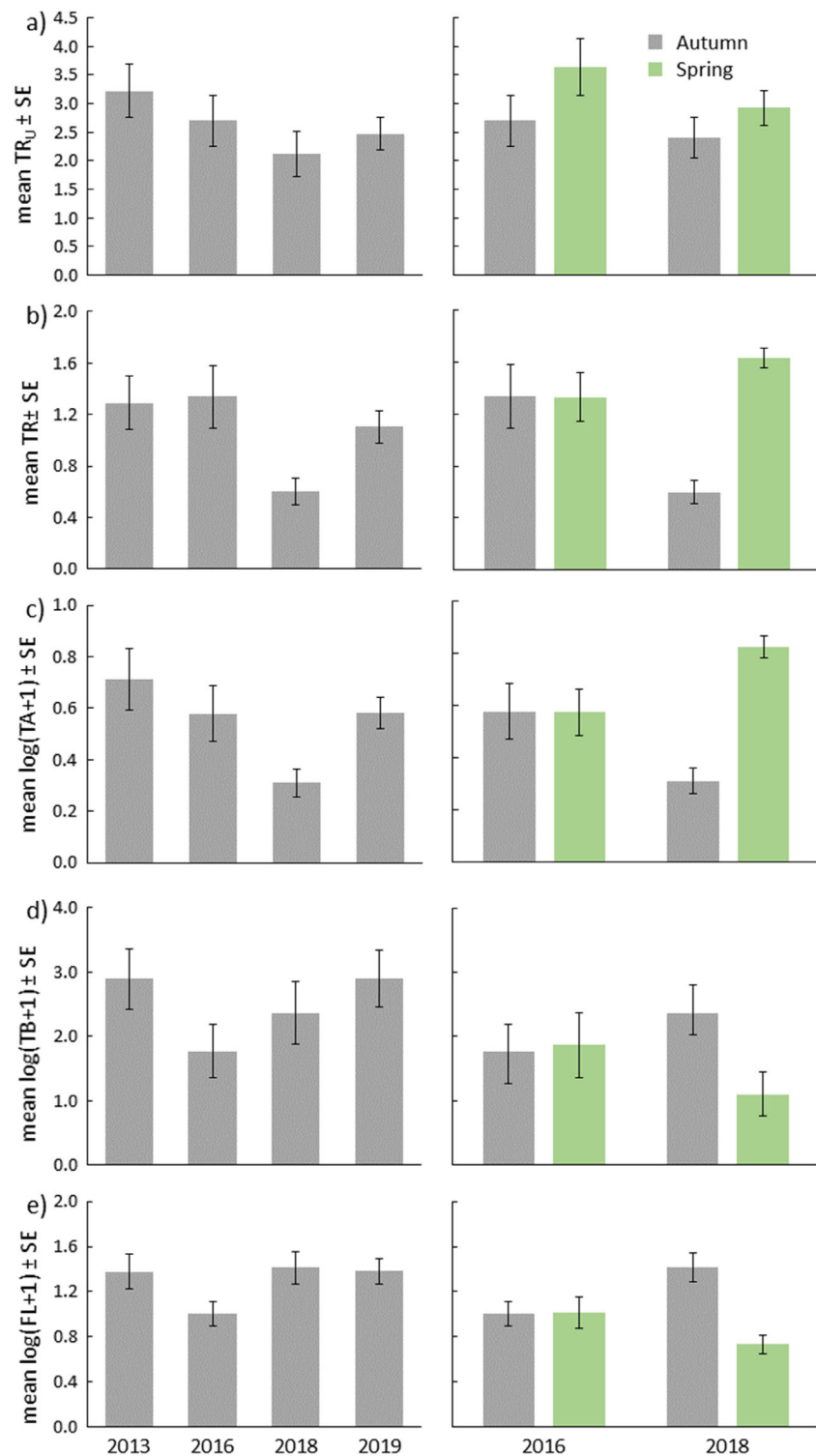


Fig. 2. Interannual (left) and seasonal (right) variation in (a) total unique taxonomic richness (TR_U), (b) mean taxonomic richness (TR), (c) mean logged total abundance (TA ; no.), (d) mean logged total biomass (TB ; kg),

(Fig. 2. *Continued*)

excluding a single minke whale *Balaenoptera acutorostrata* in autumn 2016, and (e) mean logged fork length (FL; mean log₁₀ cm), with standard error bars. There was a significant effect of year on TR and TA, while seasonal differences were significant for TR_U, TR, TA, and FL, with an interaction between year and season present for TR, TA, and FL. See Table 3 and Appendix S1: Table S2 for *P* values.

associated with higher TR_U values than autumn, regardless of year. Seasonal differences in terms of TR and logged TA were minimal in 2016 but marked in 2018, when these measures were on average 2.7 times higher in spring compared to autumn. Mean logged FL showed the opposite trend, with a mean value in spring 2018 that was half that in the autumn (0.73 ± 0.084 vs. 1.41 ± 0.14 per survey).

Species composition

Multivariate PERMANOVA indicated that the composition of the assemblages differed between years ($P \leq 0.00001$) and by season ($P \leq 0.00001$; Table 4). The CAP visualization of the multi-year autumnal logged abundance data showed separation of taxa along year gradients, although there was overlap between the assemblages in 2018 and 2019 (Fig. 3). Taxa that contributed the most to dissimilarity between years are shown using vector plots and included southern bluefin tuna *Thunnus maccoyii*, which was strongly associated with 2018, pilotfish *Naucrates ductor* and *Decapterus* scad (2013) and juvenile fishes (2016). CAP visualization of abundance data in 2016 and 2018 revealed significant seasonal shifts, with the spring surveys not only overlapping in space but also clearly distinct from the autumn assemblages. Spring assemblages were strongly associated with jacks and *Decapterus* scad, autumn 2016 with pilotfish, juvenile fishes, and wahoo and autumn 2018 with southern bluefin tuna.

Mobile megafauna were primarily observed in autumn and included southern bluefin tuna ($n = 33$; 2018/2019), common dolphin *Delphinus delphis* ($n = 7$; 2018), copper shark *Carcharhinus brachyurus* ($n = 9$; 2018/2019), northern minke whale *Balaenoptera acutorostrata* ($n = 3$; 2016), tiger shark ($n = 2$; 2019), and blue shark *Prionace glauca* ($n = 1$; 2013). In contrast, some megafauna were primarily or only observed in spring, including shortfin mako shark *Isurus oxyrinchus* ($n = 3$, spring 2016; $n = 1$, autumn 2013) and wahoo *Acanthocybium solandri* ($n = 2$; 2016).

Fine-scale spatial and temporal stability

Spatial comparisons of model predictions between the six surveys suggest that the fine-scale habitat usage patterns of pelagic taxa within the study area largely did not differ either between seasons or years (Fig. 4; Appendix S1: Fig. S2). Thirteen of the 15 SSIM values were positive, with 11 of these comparisons suggestive of relatively strong positive spatial correlation ($0.1 < \text{SSIM} < 0.6$) and three comparisons more consistent with spatial independence ($-0.1 < \text{SSIM} < 0.1$). Only one comparison (autumn/spring 2016) displayed a notably negative SSIM value (-0.2) consistent with seasonal partitioning.

DISCUSSION

Many pelagic taxa are nomadic, displaying plastic migratory schedules and long-distance (>1000s kms) movements influenced by dynamic oceanographic features (Game et al. 2009, Briscoe et al. 2016, Braun et al. 2019). A perennial criticism of pelagic MPAs remains that they are ill-suited to the life histories of the species that they purport to conserve (Le Quesne and Codling 2009, Graham et al. 2012, Gilman et al. 2019). We found that a pelagic assemblage associated with a major Indian Ocean bathymetric feature, the Perth Canyon, demonstrated temporal stability across a seven-year period, with no effect of year on total number of unique taxa, mean biomass, and mean size. Moreover, even though variation was recorded between years in taxonomic richness and abundance, pairwise comparisons confirmed that the variability was due to 2018 alone, with these values stable between the remaining sampled years.

These results add to growing evidence that Perth Canyon is a habitat that supports relatively high abundances of pelagic fishes (Bouchet et al. 2017) and aggregations of wildlife, including the pygmy and Endangered Antarctic blue whale *Balaenoptera musculus intermedia* (Double et al. 2014, Nanson et al. 2018). Our finding that the Perth Canyon pelagic assemblage is relatively

Table 3. Results of PERMANOVAs testing the effect of (A) year on total unique number of taxa (TR_U), mean taxonomic richness (TR), mean total abundance (TA), mean total biomass (TB; kg), and mean fork length (FL; cm) (one-way PERMANOVA) and (B) year and season on the same variables (two-way PERMANOVA).

Variable	df	SS	MS	Pseudo-F	P	perms
A						
TR _U						
Survey	3	6.50	2.17	1.08	0.371	800
Res	50	100.80	2.02			
Total	53	107.30				
TR						
Survey	3	4.46	1.49	4.49	0.009	999
Res	50	16.57	0.33			
Total	53	21.03				
TA						
Survey	3	1.11	0.37	5.39	0.002	999
Res	50	3.44	0.07			
Total	53	4.55				
TB						
Survey	3	4.76	1.59	1.38	0.238	999
Res	50	57.55	1.15			
Total	53	62.30				
FL						
Survey	3	0.79	0.26	1.32	0.291	998
Res	47	9.30	0.20			
Total	50	10.08				
B						
TR _U						
Season	1	9.37	9.37	4.29	0.048	33
Res	47	102.59	2.18			
Total	48	111.96				
TR						
Season	1	3.05	3.05	11.02	0.002	995
Year	1	0.54	0.54	1.95	0.173	996
SexYe	1	3.14	3.14	11.38	0.001	995
Res	45	12.44	0.28			
Total	48	20.57				
TA						
Season	1	0.74	0.74	15.00	0.002	997
Year	1	0.01	0.01	0.24	0.624	997
YexSe	1	0.85	0.85	17.20	0.001	996
Res	45	2.23	0.05			
Total	48	4.12				
TB						
Season	1	0.79	0.79	1.15	0.276	997
Res	47	32.27	0.69			
Total	48	33.06				
FL						
Season	1	1.34	1.34	11.05	0.003	995
Year	1	0.12	0.12	0.96	0.318	995
SexYe	1	0.66	0.66	5.46	0.034	998
Res	41	4.96	0.12			
Total	44	7.48				

Notes: Mean values were calculated across samples on a given string and a single minke whale *Balaenoptera acutorostrata* was excluded from TB in autumn 2016. Significant *P* values have been formatted in bold.

spatiotemporally stable adds to the location's ecological importance and suggests that strong, year-round protection (i.e., IUCN II or above) could have major conservation outcomes for pelagic wildlife.

In 2016, levels of taxonomic richness, abundance, and biomass remained high throughout the year, with a seasonal signature effectively absent. Oceanographic variability in the vicinity of the Perth Canyon is driven by the Leeuwin Current, a 100 km wide, ~300 m deep current of warm water that runs south along the coast of Western Australia. In autumn, a strong Leeuwin Current suppresses upwelling, yet cooling and storm activity destratify the water column, allowing deep, nutrient-rich water to reach the surface and cause sporadic peaks in primary productivity (Lourey et al. 2006, Koslow et al. 2008). In the spring, however, southerly winds weaken the Leeuwin Current, allowing upwelling (Rennie et al. 2009), such that the submarine canyon's attractiveness as a feeding ground for mobile megafauna may remain high throughout the year (Pattiaratchi and Buchan 1991, Feng et al. 2009, Rennie et al. 2009, Nanson et al. 2018). Indeed, our results suggest that the Perth Canyon may act as an important stopover for a range of migratory species, regardless of season. Many megafauna species, including the tiger shark, common dolphin, and southern bluefin tuna, were recorded within the study area in autumn, despite overall abundance and diversity typically being higher in spring.

The more pronounced seasonality observed in 2018, in addition to the anomalously low levels of taxonomic richness and abundance observed in this year compared to others, may reflect interactions between the Leeuwin Current and easterly wind anomalies in the equatorial Pacific (i.e., ENSO). Unlike the other sampled years, autumn 2018 was associated with an unexpected La Niña event (Zhang et al. 2019). La Niña strengthens the Leeuwin Current's flow, driving marine heatwaves, the tropicalization of temperate communities, and changes in productivity (Feng et al. 2013, Pearce and Feng 2013, Pearce et al. 2016, Hewitt et al. 2018). For example, the 2011 La Niña event raised temperatures by over 4°C and reduced chlorophyll concentrations from 1 to <0.25 mg/m³ (Chen et al. 2019). As such, the 2018 La Niña may have affected the productivity and

Table 4. Results of (A) one-way multivariate PERMANOVA testing the effect of year on relative abundances of pelagic taxa at the PCMP and (B) two-way multivariate PERMANOVA testing for the effect of both year and season.

	df	SS	MS	Pseudo-F	P	perms
A						
Year	3	15802	5267.2	4.53	0.000001	569156
Res	50	58079	1161.6			
Total	53	73881				
B						
Year	1	6511.3	6511.3	7.1537	0.00001	95235
Season	1	11205	11205	12.311	0.00001	95193
YexSe	1	4740.8	4740.8	5.2085	0.0005	95046
Res	45	40959	910.2			
Total	48	64497				

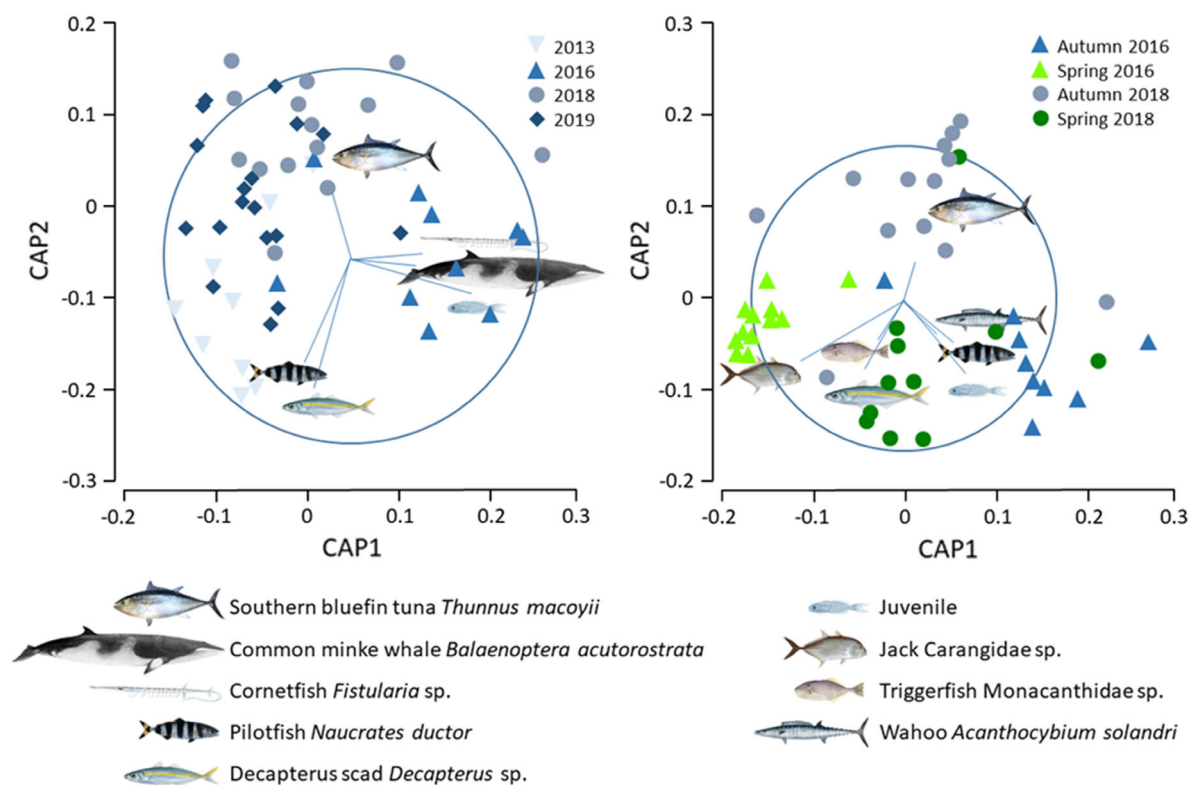


Fig. 3. Canonical analysis of principal (CAP) co-ordinates visualizing differences in taxonomic composition between (left) autumn in different years and (right) seasons in 2016 and 2018, based on a square-root-transform of abundance data and Bray-Curtis similarity matrix. Species with strong associations include the following: Decapterus scad *Decapterus* sp., jacks Carangidae sp., pilotfish *Naucrates ductor*, and southern bluefin tuna *Thunnus maccoyii*.

other characteristics of the Perth Canyon, with knock-on effects on taxonomic richness and abundance.

We also found some evidence for spatial stability in the fine-scale predicted distribution of pelagic wildlife at the head of Perth Canyon. The vast

majority of the 15 SSIM values were positive, suggesting that taxa are likely to occur in the same habitats regardless of season or year. Areas of greater probability of presence were associated with the southern and eastern borders of the IUCN IV box in addition to the less protected

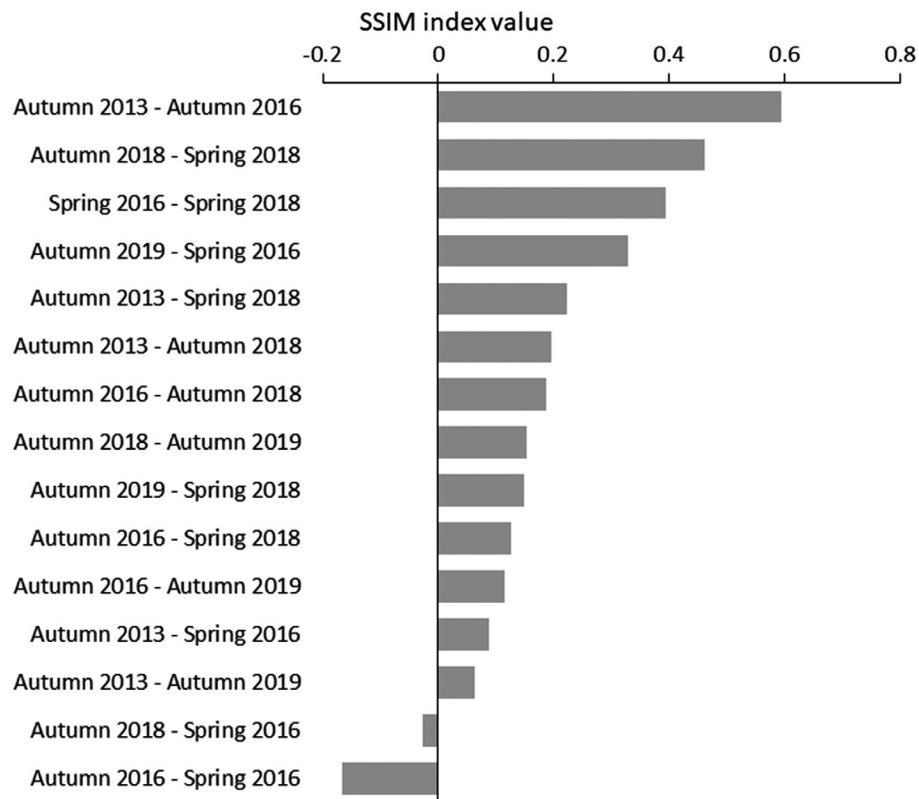


Fig. 4. Structural similarity (SSIM) index values for compared surveys. SSIM values vary between 1 and -1 , with these indicating, respectively, positive and negative spatial correlations.

southern rim of the canyon tip, where depth-integrated primary production levels are highest and krill corralled by upwellings and eddies attract foraging pygmy blue whales (Rennie et al. 2009). The only clear exception to the trend was the autumn–spring 2016 comparison, which displayed a negative SSIM value of ~ -0.2 and was more consistent with mild inter-seasonal spatial partitioning. This anomaly is plausibly related to the occurrence in the first half of 2016 of a strong El Niño event, which has been shown to weaken the Leeuwin Current and reduce prey availability in the eastern Indian Ocean, forcing mobile predators to shift offshore (Crocker et al. 2006, Koslow et al. 2008, Hill et al. 2016, Sprogis et al. 2018). The high abundance and taxonomic richness values observed in the canyon head in 2016 are also consistent with it potentially having an ecological function as a megafauna refuge during environmentally challenging years (Yoklavich et al. 2000).

The strong interannual stability demonstrated by the pelagic assemblage at the Perth Canyon head appears to have masked underlying changes in taxonomic composition. For example, pilotfish and *Decapterus* scad were strongly associated with 2013 and 2019, whereas juvenile fishes were more closely associated with 2016 and southern bluefin tuna with 2018. The CAP plots were also consistent with high seasonal turnover in taxa composition, with clear separation between spring and autumn assemblages and strong, seasonal associations of jacks and *Decapterus* scads with spring. Autumns were primarily associated with southern bluefin tuna and juvenile fishes, consistent with previous studies suggesting that recruitment increases with strong Leeuwin Current flows (Pearce et al. 2016). While a degree of taxonomic turnover at this pelagic hotspot is consistent with prey patchiness as an important pelagic influence on predator abundance (Benoit-Bird et al. 2013, Ainley et al. 2017),

we note that our results also demonstrated inter-annual stability in the total unique number of taxa at the PCMP. As such, it appears that the canyon head remains a pelagic biodiversity hotspot despite changes in the dominant taxa from year to year.

A caveat to our results is that our sampling design was limited to the Austral autumn and spring and thus can only provide seasonal snapshots of the PCMP assemblage. While these snapshots were compiled over a relatively long time period and focused on a data-deficient area, monthly sampling would have enabled a more robust understanding of seasonal variability. Moreover, although mid-water stereo-BRUVS are an effective, non-destructive methodology available to quantify remote, patchy pelagic assemblages (Letessier et al. 2015), their ability to detect is a function of deployment depth and bait type, with the biases surrounding the use of BRUVS described in detail in Bouchet and Meeuwig (2015). Thus, interpretation of our MaxEnt results is vulnerable to issues surrounding imperfect detectability, such that the failure to detect a species does not necessarily equate to true absence (Bouchet and Meeuwig 2015, Jones et al. 2019). Our surveys will not have detected all taxonomic groups present at the canyon, particularly rare or low-abundance species; however, the taxa accumulation curve suggests that all major groups are likely represented.

Another potential criticism of our study may be that our sampling effort was insufficient to detect differences between seasons and years; however, we conducted post hoc power analyses, following Cohen (1988). We note that in the case of total number of unique taxa, which had the least significant P value (0.39) for the between-year ANOVA, the effect size, f , was 0.14, indicating that our detectable effect size was closer to small ($f = 0.1$) than medium ($f = 0.25$; Cohen 1988) given the sample sizes and variances in each survey. As such, the stability observed was unlikely to be a type II error where we failed to see interannual and seasonal differences.

There are over 9000 submarine canyons globally, measuring over 25,000 km in cumulative length (Huang et al. 2014, Fernandez-Arcaya et al. 2017). In Australia alone, there are 713 submarine canyons, 95 of which are shelf-incising

(Huang et al. 2014). Despite their ecological importance, it was estimated in 2014 that just 8% of submarine canyons in southeastern and southwestern Australia were protected by Australian Marine Parks (AMPs), declining to 1% in the north (Huang et al. 2014). Protection of these keystone structures is dwindling rather than increasing: In 2018, the main Perth Canyon head was stripped of its IUCN II status and downgraded to IUCN IV in order to “improve access to important fishing areas,” with the original IUCN II zone transplanted to a smaller head approximately 40 km further offshore (South-west Marine Parks Network Management Plan 2018).

Strengthening protection within the PCMP could improve conservation outcomes for a range of pelagic wildlife. Many species appear to use the canyon both across seasons and years, with the Critically Endangered southern bluefin tuna, for example, observed in both 2018 and 2019, while pygmy blue whales have been observed for durations of roughly a month during the summer (Double et al. 2014, Nanson et al. 2018). Yet the region around Perth is subject to high levels of recreational fishing relative to other parts of the Western Australian coast, and the PCMP is the target of a growing charter-based fishing industry (Ryan et al. 2015). Strengthening protection at the PCMP would therefore protect associated wildlife from area-specific stressors, consistent with Kerwath et al. (2008).

Moreover, many migratory species in the region experience multiple stressors along their ranges, including acoustic pollution from shipping (i.e., Double et al. 2014), thus improved protection at the PCMP may provide a haven from cumulative, sub-lethal threats, consistent with Game et al. (2009). Lastly, there is evidence that large MPAs such as the British Indian Ocean Territory MPA (BIOT; 640,000 km²) and the proposed Sea of the Hebrides MPA (10,325 km²) encompass the majority of the activity ranges of some mobile species (Doherty et al. 2017, Richardson et al. 2018, Carlisle et al. 2019). Although the PCMP (7409 km²) is not as large as BIOT MPA, it is similar in size to the Sea of Hebrides MPA and may therefore provide some protection for some mobile species with limited movement rates.

Spatial modeling showed that areas of greater probability of presence occurred not just in the IUCN VI zone but also in the least protected (IUCN V) waters at the southern rim of the canyon. This finding indicates that the current zoning plan may be incommensurate with the conservation value of the PCMP to pelagic wildlife populations, and suggests that IUCN II zoning should be reinstated to the majority of the canyon head. The precautionary principle states that conservative action is prudent when uncertainty levels are high (Falcu 2016). Although we did not examine the broader PCMP assemblage directly, it could be argued that the entire length of the submarine canyon extending to the EEZ should also receive higher levels of protection. This is especially true as despite strong fisheries governance in Australia, targeted fish populations have declined by one third in a decade (Edgar et al. 2018) and pelagic sharks have declined by over 70–90% in 50 yr (Roff et al. 2018). Stronger protection of locations predictably used by ocean wildlife is necessary to protect all life stages along their transoceanic journeys (Boerder et al. 2019). Submarine canyons such as the PCMP are clear candidates for strong protection if we are to halt and reverse declines in pelagic wildlife.

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